DISTRIBUTION AND ECOLOGY OF CAVERNICOLOUS COLEOPTERA IN BAT CAVE, CARTER COUNTY, KENTUCKY

A Thesis

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Master of Science

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by

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Accepted by the faculty of the School of Sciences and Mathematics, Morehead State University, in partial fulfillment of the requirements for the Master of Science degree.

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ABSTRACT OF THESIS

DISTRIBUTION AND ECOLOGY OF CAVERNICOLOUS COLEOPTERA IN BAT CAVE, CARTER COUNTY, KENTUCKY

Cavernicolous Coleoptera in Bat Cave were studied to determine their intra-cave distributional patterns. Beetles were collected by pitfall trapping, visual survey, and Berlese extraction. Temperature and relative humidity were monitored at nine stations throughout the cave to determine their influence on beetle distribution. Stream-bank detritus and bat guano deposits were observed to determine their influence on beetle distribution.

Of 26 beetle taxa collected, only four were abundant. All four were associated primarily with bat guano deposits in the cave's upper level or in the main hibernation room. Of these, *Aglenus* sp. and *Prionochaeta opaca* were restricted to a single room; *Aleochara* sp. and *Atheta* sp. occurred throughout the cave and exhibited marked niche separation. The other 22 taxa were found less frequently and were primarily associated with stream-bank detritus in the lower level; most were considered to be accidentals.

David Bruce Conn
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28 April 1980
Date

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TABLE OF CONTENTS

LIST OF TABLES

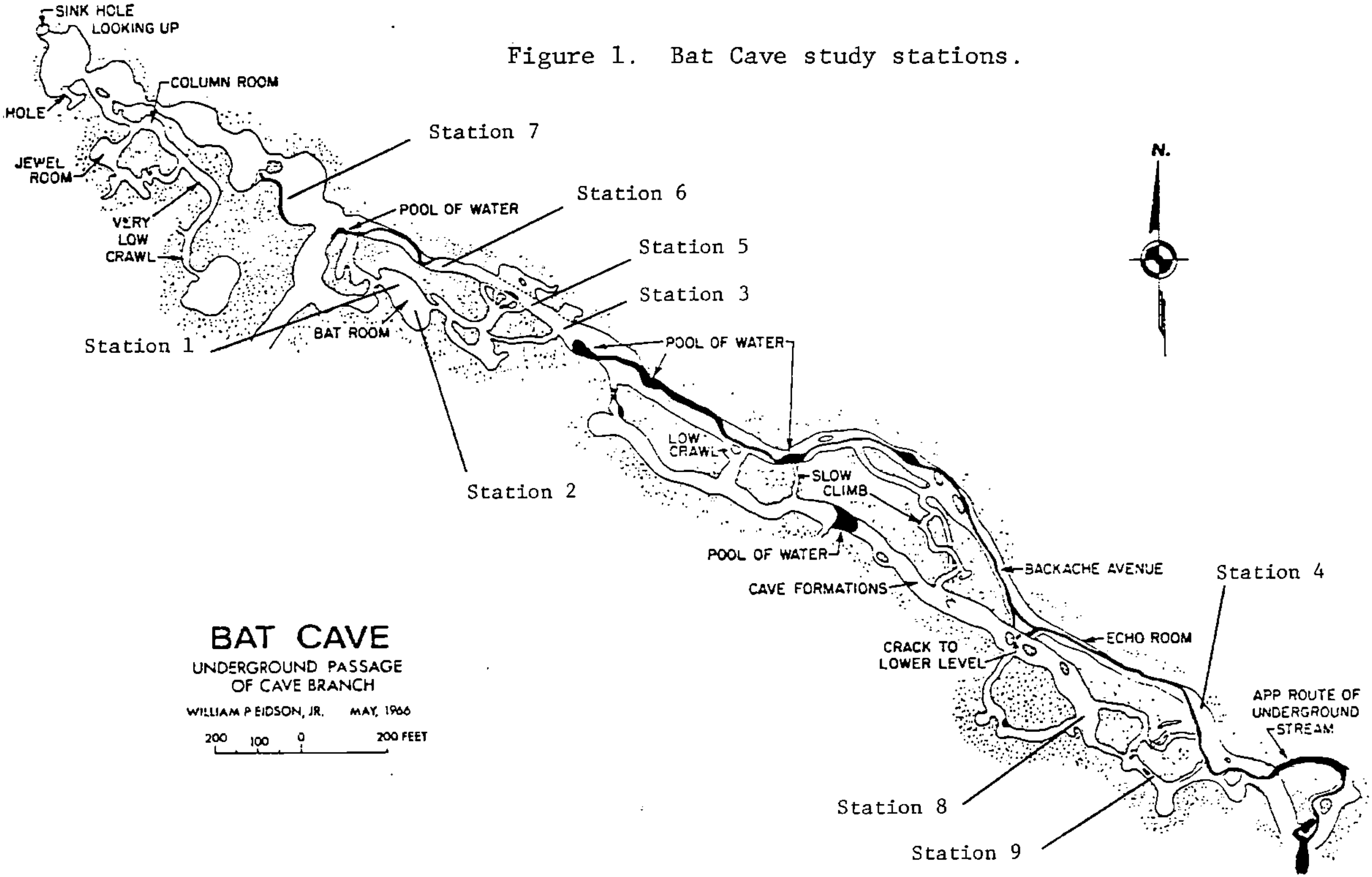
LIST OF ILLUSTRATIONS

INTRODUCTION

Environmental conditions influencing the activities of epigean populations differ greatly from those affecting cavernicolous biota. The physical environment in a cave is relatively stable with respect to temperature, relative humidity and photic effects. Energy flow into a cave ecosystem in the form of food available for animal consumption is usually sparse and sporadic. Photosynthesis is impossible in the aphotic zone; food input must come by way of seepage, stream flooding or transport by trogloxenes. These extraneous organic materials, and the fungi growing on them serve as an important food source for many cavernicoles.

Bat Cave, a tunnel cave developed in St. Louis and Ste. Genevieve limestone (McGrain 1966), is approximately 1030 m long and has over 2100 m of accessible passageway, as mapped by Eidson (1966). Bat Cave has two entrances and two main levels (Figure 1). The upper level is dry and has a clay loam floor with some rimstone pools and flowstone; the lower level is primarily a stream channel for Cave Branch, a tributary of Tygart's Creek. Bat Cave is situated near the center of Carter Caves State Park, with its downstream entrance at 83° 07' 38" west longitude and 38° 22' 41" north latitude (U. S.

Figure 1. Bat Cave study stations.



Geological Survey 1962).

Although Bat Cave has a physical environment similar to that in caves of comparable size and structure, it has unique biotic characteristics. One such characteristic is the occurrence of a large population of the Indiana Bat, *Myotis sodalis*. This hibernating population of *M. sodalis* is one of the largest in the world, having been estimated at nearly 100,000 individuals (Hassell 1967). Although most of the bats are not present during the summer, several hundred remain in the cave year-round. Through guano deposition and periodic die-off, the bats provide an important food source to terrestrial cavernicoles.

In this research, both spatial and temporal distributions of cavernicolous Coleoptera in Bat Cave were studied. The influence of various physical and biotic parameters on beetle distribution were investigated, with emphasis being placed on bat activity. Most similar work by other investigators has been entirely qualitative; the paucity of quantitative data made this study important to understanding cave ecosystems. Because the cave fauna of Carter Caves has received little attention from ecologists, this study is important in providing a basis for future studies of cavernicolous invertebrate ecology in Carter Caves.

LITERATURE REVIEW

Factors Affecting Cavernicole Distribution

Temperature and moisture have been the most commonly investigated physical factors influencing cavernicole distribution. Barr (1958), studying cavernicolous arthropods in general, presented data suggesting that both factors were important; he elaborated on that in later discussions of cave ecology (Barr 1967, 1968). Christiansen et al. (1961) found cave Collembola most abundant in areas with 20-29% soil moisture. Mitchell (1965) suggested that *Rhadine subterranea* was neither highly stenohygrobic nor highly stenothermic, though his data indicated strong preference for a saturated atmosphere and a specific temperature range. McKinney (1974) suggested that temperature may affect the abundance of *Pseudanophthalmus menetriesi*, *P. pubescens* and *P. striatus*. His data showed decreased longevity for all three species at 85% relative humidity, with *P. menetriesi* being least affected; when given a choice, all three preferred the wettest substrate moisture. Poulson and Culver (1969) showed no significant correlation between cave arthropod species diversity and soil moisture content or atmospheric index of evaporation.

Other physical factors affecting cavernicole distribution have been less studied. Collembolan abundance was shown to be greatest where substrate particle size was between 0.119 mm and 0.03 mm (Christiansen et al. 1961). McKinney (1974) suggested that the abundance of three Pseudanophthalmus species was positively correlated with substrate complexity. High environmental stability, low intensity of flooding and high substrate diversity have been shown to correlate positively with arthropod species diversity in caves (Poulson and Culver 1969). In a study of terrestrial cave arthropods, Peck (1976) found faunal abundance greatest in the deep crepuscular zone and discussed the possible influence of the cave entrance on cavernicole distribution.

Substrate organic content may be considered a physico-biotic factor in determining terrestrial cavernicole distribution, thus relating absolute physical and biotic factors. It has been shown that substrate organic content is positively correlated with abundance (Christiansen et al. 1961) and diversity (Poulson and Culver 1969) of cavernicolous arthropods.

Cavernicolous animals are like epigean forms in being limited in distribution by food availability. This has been widely regarded as the most important single factor influencing cavernicole distribution (Barr 1967, 1968). Xylophagous arthropods and their predators have generally exhibited an aggregated distribution coinciding with stream-borne plant detritus (Hawes 1939; Barr 1958; McKinney 1974; Kane and Poulson 1973, 1976). An aggregated pattern has also been demonstrated for guanobic communities (Calder and Bleakney 1965; Barr 1958; Poulson 1972). Troglobitic carabids that prey on eggs and nymphs of cave crickets have been seen most often in areas where loose substrate permitted cricket oviposition. This has been reported by Mitchell (1965) for Rhadine subterranea, by Kane and Poulson (1973, 1976) for Neaphaenops tellkampfii and by Marsh (1969) for Darlingtonea kentuckensis.

Studies of how soil antibiotics affect terrestrial troglobites have been briefly reviewed by Poulson and White (1969) and by Poulson (1975). Those studies, dealing mostly with leptodirids (catopids), suggested that local populations must adapt to avoid attack by microflora in the cave soil. That adaptation, or a lack of it, could determine the distribution of some species.

Seasonality in terrestrial cave faunal cycles has been investigated by several biologists. Poulson (1972) reviewed literature pertaining to cycles induced by seasonal bat activity. In a symposium on cave beetle life cycles (see introduction by Poulson 1975), it was emphasized that many troglobitic carabids that prey on cricket eggs showed seasonal population peaks coinciding with maximum oviposition by crickets. In an earlier study, McKinney (1974) suggested that fluctuations in populations of three Pseudanophthalmus species were due to temperature differences and differences in litter fauna at various stages of litter decomposition. Ives' (1951) conclusions regarding faunal abundance cycles in a crepuscular cave are probably not applicable to aphotic biota because much crepuscular biota is present only for overwintering.

Cavernicolous Coleoptera of Carter County

Carter County caves have been visited by biospeleologists for many years. Except for bat studies in Bat Cave, all studies were brief faunal surveys. Several investigators have reported the presence of beetles in the caves. Harker and Barr (1979) cited much of that literature, and it is from their report that the information from Bolivar and Jeannel (1931) was obtained for the present study. Because of the nature of their study, Harker and Barr mentioned only the literature pertaining to original observations; they did not review later references to those observations.

The beetle species reported from Carter County caves are listed below by family.

Brathinidae

Brathinus nitidus LeConte

Bat Cave (Barr 1958).

Carabidae

Amara muscula Say

Cascade Cave (Bolivar and Jeannel 1931).

Bembidion picipes (Kirby)

Bat Cave (Bolivar and Jeannel 1931). Harker and Barr (1979) considered this as probably synonymous with *B. wingatei* Bland.

Bembidion wingatei Bland

Bat Cave (Harker and Barr 1979).

Calathus opaculus LeConte

Cascade Cave (Bolivar and Jeannel 1931).

Agonum angustatus (Say)

Cascade Cave. According to Harker and Barr (1979), who reported this as a synonym, *Platynus angustatus* Say, Jeannel reported a synonym, *P. cervicalis* Casey.

Agonum tenuicollis (LeConte)

Bat Cave (Harker and Barr 1979). Reported as as synonym, *Platynus tenuicollis* LeConte.

Pseudanophthalmus packardi Barr

Bat Cave (Barr 1958, 1959; Harker and Barr 1979). Counterfeiters, Cow, Horn Hollow, Iolanthe and Jarvie Roarks caves (Harker and Barr 1979). Barr (1959) described this species from the type series which he collected in Bat Cave. Earlier (1958), he referred to this species as Pseudanophthalmus n. sp. #5 in an unpublished doctoral thesis. In both reports, he stated that P. packardi was undoubtedly the beetle collected from X Cave by Packard (1888) and erroneously identified as Anophthalmus pusio Horn by LeConte. Pseudanophthalmus pusio (Horn), the legitimate synonym for A. pusio Horn, is known only from Earhart's Cave, Virginia (Nicholas 1960). Garman's (1892) reference to A. pusio from Carter County caves is probably based on Packard's (1888) observations. Barber (1931) reported the occurrence of P. pusio in Carter Caves; he cited Packard (1888) as the source of that information, but also indicated that LeConte's identification was incorrect. Barber reported in the same paper that Packard's specimens of this beetle from Carter Caves had been lost.

In his checklist of United States troglobitic animals, Nicholas (1960) listed P. packardi as known only from the type locality.

Pseudanophthalmus pusio (Horn)

X Cave (Packard 1888). Reported as a synonym, Anophthalmus pusio Horn. See entry for P. packardi above.

Pterostichus honestus (Say)

Bat Cave (Bolivar and Jeannel 1931).

Leptodiridae

Catops gratiosus (Blanchard)

Bat Cave (Barr 1958).

Prionochaeta opaca (Say)

Bat Cave (Peck 1977).

Packard (1888) reported an "undetermined eyeless coleopterous larva" from Bat Cave. Dearolf (1953) made a brief survey of the invertebrates in Cascade Cave, but did not report finding any beetles. In that same study, Dearolf surveyed the invertebrates of "Bat Cave, Ky." and "Laural Cave, Ky."; but his reported collection dates, when compared to his itineraries, indicate that those references are to Central Kentucky caves.

MATERIALS AND METHODS

Visits to Bat Cave were made between 11 July 1979 and 29 March 1980; visits were made weekly during most of the period. Field study began during *Myotis sodalis* summer population activity and continued through the arrival, hibernation and early dispersal periods of the *M. sodalis* winter population. Field work was restricted to the aphotic zone of Bat Cave.

To avoid experimental bias, three methods were used to collect beetles: (1) visual survey; (2) Berlèse extraction; (3) pitfall trapping. Endogenous and cursorial beetles were collected by visual survey, including searching under rocks, logs and detritus. Sedentary edaphic beetles were collected by Berlèse extraction, as were some vagile forms.

Because many cavernicoles are cryptic in habit, pitfall traps similar to those described by Barber (1931) were used. These traps were designed primarily to attract scavengers. Each trap was set by burying a 4 cm x 10 cm glass vial in the cave floor, leaving the rim flush with ground level. Bait, approximately 5 g of spoiled pork liver, was wrapped in cheesecloth and hung into the vial from 6 mm mesh hardware cloth. Galt's solution, a non-repellent narcotizing and temporary preserving agent, was put into each vial. A pitfall trap was set at each of nine stations established at various points in the cave (Figure 1). On each visit, each trap was emptied and reset. Bait was replaced only when odor was no longer evident, ensuring attraction of beetles feeding on carrion at successive stages of decomposition and those feeding on fungi growing on the bait. To survey beetles from various habitats within Bat Cave, the nine stations were established in areas with differing physical features.

Station 1, located in a large room in the cave's upper level, had a substrate of clay loam and breakdown blocks. Wet-weather seepage provided the only water input to this room. As in previous years (Hassell 1967), several hundred bats occupied this room throughout the summer, leaving large guano deposits within 1-2 m of the trap.

Station 2, located about 10 m from Station 1, had a substrate of clay and breakdown blocks. This station's trap was nearly 9 m from the nearest guano bed and was separated from it by a 2-m-wide by 1-m-deep ditch.

Station 3, located in the cave's lower level, had a substrate of thick piles of partially decomposed plant detritus lying atop large breakdown blocks. Detritus accumulation apparently resulted from extreme flooding of Cave Branch which flows through the breakdown blocks 5 m below this station.

Station 4, located in the main *M. sodalis* hibernation room, had a substrate of small stones and streambed gravel. Cave Branch flowed approximately 10 m from this station, but deposited no plant detritus there. Although several thousand bats overwintered within a few meters of this station, their torpid state minimized guano deposition.

Station 5, located about 15 m upstream from Station 3 and 2.5 m above Cave Branch, had a substrate of clay loam atop breakdown blocks, with stream-deposited plant detritus scattered in a thin layer. This station was within 5 m of large detritus piles.

Station 6, located on the bank of Cave Branch, had a substrate of alluvial sand. The entire area was flooded periodically, resulting in much physical scouring, but little detritus deposition.

Station 7, located in a large upper level room, had a firmly packed clay floor. An intermittent trickle flowed 2 m from the trap. A small amount of wood was scattered about, apparently from human activity. Some guano deposition occurred from bat activity in the passage west of this site.

Station 8, located in an upper level room, had a clay loam substrate. A few small trickles occurred here during heavy rainfall. Bat activity, with associated guano deposition, was moderate in this area throughout the winter. Much bat activity, with substantial guano deposition, occurred throughout the winter in a side passage several meters from this site.

Station 9, located in a passage connecting the upper and lower levels, had a clay substrate. Several shallow pools were within 1-2 m of this site. No organic deposits were observed here, though the abundance of troglobitic amphipods and planarians in the pools indicated that some organic material was available.

Temperature and relative humidity at each station were measured on each visit, using a Bendix Friez Psychron psychrometer, Model 566-2. Mean temperature and relative humidity were calculated for each station. Standard deviations from those means were used as indices of environmental stability.

Casual observations of bat activity and location were made during each visit to Bat Cave, but no quantitative measurements were made. The observations of Hassell (1967) and Hardin (1967) were used to predict approximate bat movements and concentrations. Throughout the hibernation period, great care was taken not to arouse the bats.

Beetles collected were preserved in 70% ethanol. Some small forms were bleached in 30% NaOH, cleared in clove oil and mounted in Kleermount for compound microscopy. Arnett's (1968) scheme was used for classification to family and genus; various group revisions were used for specific identification. Larvae were identified with Peterson's (1960) key. All beetles were deposited in the Morehead State University Entomological Collection.

RESULTS

Temperature and relative humidity data for the nine study stations are listed in Table I. Standard deviations are meaningful as indices of environmental stability only when viewed in relation to one another; there is no base level for comparison.

All beetles collected in Bat Cave during the present research are listed below by family. The total number of specimens collected and general collection locations are listed. A single asterisk (*) preceding a name indicates the first report of that taxon from Carter County caves. Unless stated otherwise, all specimens were adults.

Brathinidae

Brathinus nitidus LeConte

2 specimens. Stream-bank detritus.

*Cantharidae

*Cantharid larvae

3 specimens. Traps 3,6,9.

Carabidae

Carabid larvae

4 specimens. Stream-bank detritus.

Table I. Temperature and relative humidity at Bat Cave study stations.

Station	Mean Temperature (°C.)	Temperature Standard Deviation	Mean Relative Humidity (%)	Relative Humidity Standard Deviation	Number of Measurements Taken
1	14.6*	1.35	96	2.9*	22
2	14.6*	1.39	96	3.2	22
3	12.7	1.01	94	4.3	21
4	11.1	1.86*	87*	9.4*	21
5	12.8	1.08	94	4.5	20
6	12.7	1.16	94	5.5	20
7	12.9	1.20	94	5.8	20
8	11.9	0.77*	94	4.1	18
9	11.1	1.27	91	5.9	18

* These data are outside of one standard deviation from the sample mean.

Agonum sp. #1 (genus _Agonum_ Bonelli)

8 specimens. Traps 1,4,6; stream-bank detritus.

Agonum sp. #2 (genus _Agonum_ Bonelli)

1 specimen. Stream-bank detritus.

Bembidion wingatei Bland

9 specimens. Stream-bank detritus.

*_Clivina_ sp. (genus _Clivina_ Latreille)

1 specimen. Stream-bank detritus.

*_Dyschirius_ sp. (genus _Dyschirius_ Panzer)

1 specimen. Stream-bank detritus.

*_Omophron americanus_ Dejean

1 specimen. Trap 6.

Pterostichus sp. (genus _Pterostichus_ Bonelli)

1 specimen. Trap 4.

*Colydiidae

*_Aglenus_ sp. (genus _Aglenus_ Erichson)

128 specimens (88 adults; 40 larvae). Summer guano piles near Station 1.

*Histeridae

*_Dendrophilus_ sp. (genus _Dendrophilus_ Leach)

1 specimen. Trap 3.

Leptodiridae

*_Nemadus horni_ Hatch

3 specimens. Traps 3,5.

Prionochaeta opaca (Say)

116 specimens. Traps 1,2; summer bat room.

*Nitidulidae

*_Glischrochilus fasciatus_ (Olivier)

3 specimens. Traps 3,5.

*Pselaphidae

*_Batrisodes_ sp. (genus _Batrisodes_ Reitter)

4 specimens. Stream-bank detritus.

*Ptiliidae

*_Ptenidium_ sp. (genus _Ptenidium_ Erichson)

7 specimens. Traps 3,4; stream-bank detritus.

*Scydmaenidae

*_Scydmaenus_ sp. (genus _Scydmaenus_ Latreille)

1 specimen. Stream-bank detritus.

*Staphylinidae

*Staphylinid larvae

170 specimens. Trap 8.

*_Aleochara_ sp.

56 specimens. Traps 1,2,4,5,6,7,8,9; summer bat room.

*<u>Atheta</u> sp.

213 specimens. Traps 1,2,3,4,5,6,8,9; winter guano piles; stream-bank detritus; bat carcasses in lower level.

*<u>Homaeotarsus</u> sp. (genus <u>Homaeotarsus</u> Hochhuth)

1 specimen. Trap 4.

*<u>Psephidonus</u> sp. (genus <u>Psephidonus</u> Gistel)

1 specimen. Trap 6.

*<u>Quedius</u> sp. #1 (genus <u>Quedius</u> Stephens)

1 specimen. Trap 7.

*<u>Quedius</u> sp. #2 (genus <u>Quedius</u> Stephens)

3 specimens. Traps 7,9; stream-bank detritus.

*<u>Stenus</u> sp. (genus <u>Stenus</u> Latreille)

2 specimens. Stream-bank detritus.

*<u>Tachinus</u> sp. #1 (genus <u>Tachinus</u> Gravenhorst)

4 specimens. Traps 3,5,7; stream-bank detritus.

*<u>Tachinus</u> sp. #2 (genus <u>Tachinus</u> Gravenhorst)

1 specimen. Trap 5.

The only beetles collected in numbers large enough to be statistically evaluated were <u>Prionochaeta opaca</u>, <u>Aglenus</u> sp., <u>Aleochara</u> sp., <u>Atheta</u> sp. and larval staphylinids. The number of <u>P</u>. <u>opaca</u>, <u>Aleochara</u> sp. and

Atheta sp. collected in each trap are listed in Table II. *Aglenus* sp. and staphylinid larvae were not included in Table II because each was collected at only one location.

Other invertebrates collected during this research are listed in the Appendix.

Table II. Numbers of *Aleochara* sp., *Atheta* sp. and *Prionochaeta opaca* collected per trap per day at Bat Cave study stations.

Trap	*Aleochara* sp.	*Atheta* sp.	*P. opaca*
1	0.04	0.01	0.39
2	0.06	0.01	0.10
3	0.00	0.12	0.00
4	0.03	0.41	0.00
5	0.01	0.22	0.00
6	0.01	0.02	0.00
7	0.07	0.00	0.00
8	0.17*	0.79*	0.00
9	0.03	0.01	0.00

* These data are outside of one standard deviation from the sample mean.

DISCUSSION

Classification of Cavernicolous Coleoptera in Bat Cave

The beetle taxa collected in this study are thought to represent 26 species, although some were not identified to species level because keys were unavailable.

Of the 26 species collected, 19 were found less than five times and considered to be accidentals in Bat Cave. Most of the accidentals were collected within short periods following flooding of Cave Branch. Except for one cantharid larva, one *Quedius* sp. #1, two *Quedius* sp. #2 and one *Tachinus* sp. #1, all 19 were collected from the main stream level.

There is evidence indicating that at least five of the species regarded as accidentals in this study are actually more common in caves than these data imply. *Brathinus nitidus* was collected only twice, but has often been found in caves throughout the southeastern United States (Barr 1960) and has been collected in Bat Cave prior to this study (Barr 1958; Harker and Barr 1979). As an epigean riparian form, *B. nitidus* is probably subject to frequent transport into Bat Cave by flood waters of Cave Branch; but, repeated occurrence of this species in caves may indicate a trogloxenous habit.

Pterostichus sp. was collected only once, but the genus is often found in Nearctic caves (Barr 1964). Bolivar and Jeannel (1931) found *P. honestus* in Bat Cave. Though common in epigean habitats, *Pterostichus* is probably a threshold trogloxene.

Batrisodes sp. was collected four times, always by Berlèse extraction from stream-bank detritus. This species is probably more common in Bat Cave than these data indicate; their small size and lack of attraction to trap baits make them difficult to find. This genus is common in caves and includes many troglophilic and troglobitic species (Park 1960).

Although *Quedius* spp. were collected only four times, the genus is common in many caves throughout the eastern United States (Ives 1930; Barr 1960; Harker and Barr 1979). Some species of this genus are considered to be very successful troglophiles, but this report is the first record for *Quedius* in an eastern Kentucky cave.

Ptenidium sp., *Agonum* sp. #1 and *Bembidion wingatei* were collected seven, eight and nine times, respectively; all three were collected throughout the study period, with no obvious seasonality.

Ptenidium sp. was always collected near stream-bank detritus in the lower level. The genus is a common epigean group and is generally found in decaying plant material. The regular occurrence of *Ptenidium* sp. in Bat Cave and the fact that two of those collected were tenerals, suggests that this species is a facultative troglophile, although it has never been reported as such.

Agonum sp. #1 was collected in the upper and lower cave levels, and was usually close to large organic deposits. *Agonum* is common in eastern Nearctic caves and some species are considered to be habitual trogloxenes (Barr 1964) or troglophiles (Harker and Barr 1979). Prior to this study, *A. angustatus* and *A. tenuicollis* were collected in Cascade and Bat caves, respectively (Harker and Barr 1979).

Bembidion wingatei was found throughout the study period and was always associated with stream-bank detritus. It has been found in Bat Cave by other investigators and was reported by Harker and Barr (1979) as common in Bat Cave. Although common in epigean habitats, *B. wingatei* is probably a troglophile. This supposition is supported by the finding of a teneral in this study; it is in agreement with Barr's (1964) opinion regarding *B. wingatei*.

Four beetle species, *Prionochaeta opaca*, *Aglenus* sp., *Aleochara* sp. and *Atheta* sp., occurred in Bat Cave as well-established troglophilic populations. This is the first report of a large thriving population of each of these taxa in eastern Kentucky caves. Peck (1977) reported such populations of P. opaca in eastern Nearctic caves, but gave no specific localities.

Prionochaeta opaca was abundant in the summer bat room throughout the fall. Only adults were collected, including a single teneral. Peck (1977) found P. opaca in Bat Cave and stressed that this species is a common troglophile throughout the southeastern United States, but is also abundant in epigean habitats.

The Aglenus sp. population, collected only by Berlèse extraction, included many tenerals, larvae and well-developed adults. Seasonality was not apparent; however, to avoid depleting the population, no Berlèse extractions were made after October. Although blind and depigmented, Aglenus is represented in epigean habitats, indicating that the species in Bat Cave may not be truly troblobitic. It is odd that this species is very abundant in one area of Bat Cave and completely absent from all other areas; facultative troglophiles are usually more generalized in their intra-cave distribution.

Aleochara sp. and Atheta sp. were abundant in Bat Cave, occurring in highest densities near Station 8. Large numbers of staphylinid larvae also occurred near Station 8 and may have represented both species.

Atheta sp. was the most common beetle in Bat Cave.

Pseudanophthalmus packardi, the only troglobitic beetle known to occur in Bat Cave, was not encountered. According to Barr (pers. comm. 1979), this rare carabid is difficult or impossible to find except at certain times of the year; he (Barr 1959) first found it in late May. No field work was done for this study during that month. *P. packardi* generally occurs near stream-bank detritus and has been found in several Carter County caves; it has never been confirmed to occur outside of Carter County (Harker and Barr 1979).

Distributional Relationships of Bat Cave Coleoptera

The large population of *Aglenus* sp. in Bat Cave seems to be limited in distribution primarily by food supply, occurring only in the fresh summer guano beds supporting fungal growth. Its absence from other guano deposits may indicate either seasonality or limitation by other environmental factors. The summer bat room is characterized by high temperature with high and stable relative humidity compared to other areas of Bat Cave (Table I); these may be limiting factors. Although Berlèse samples were not taken from the guano beds to determine seasonality of the *Aglenus* sp. population, the presence of all life cycle stages in fall samples suggests year-round reproductive activity.

Except for its greater vagility, *Prionochaeta opaca* has a distribution in Bat Cave similar to that of *Aglenus* sp. This similarity may result from both groups being restricted to similar environmental optima. Seasonality is probably more important in determining *P. opaca* distribution in Bat Cave; epigean populations of *P. opaca* are highly seasonal (Peck 1977). *P. opaca* is a generalized scavenger on decaying animal matter, and large fresh guano deposits coinciding with seasonal activity of *P. opaca*, occurred only in the summer bat room. The higher *P. opaca* density at Trap 1 as compared to Trap 2 was probably due to the close proximity of Trap 1 to the beetle's normal food supply.

Although *Aleochara* sp. and *Atheta* sp. are closely related (subfamily Aleocharinae), their distributions within Bat Cave were significantly different (chi-square = 90.77; 8 degrees of freedom). Both had density maxima at Trap 8, but elsewhere their populations had little overlap (Table II). Both species were active throughout the study period, indicating that separation was not temporal. Spatial analysis shows that 88% of *Aleochara* sp. and only 48% of *Atheta* sp. occurred in the cave's upper level (Figures 2 and 3). Densities for both species at Trap 8 were significantly

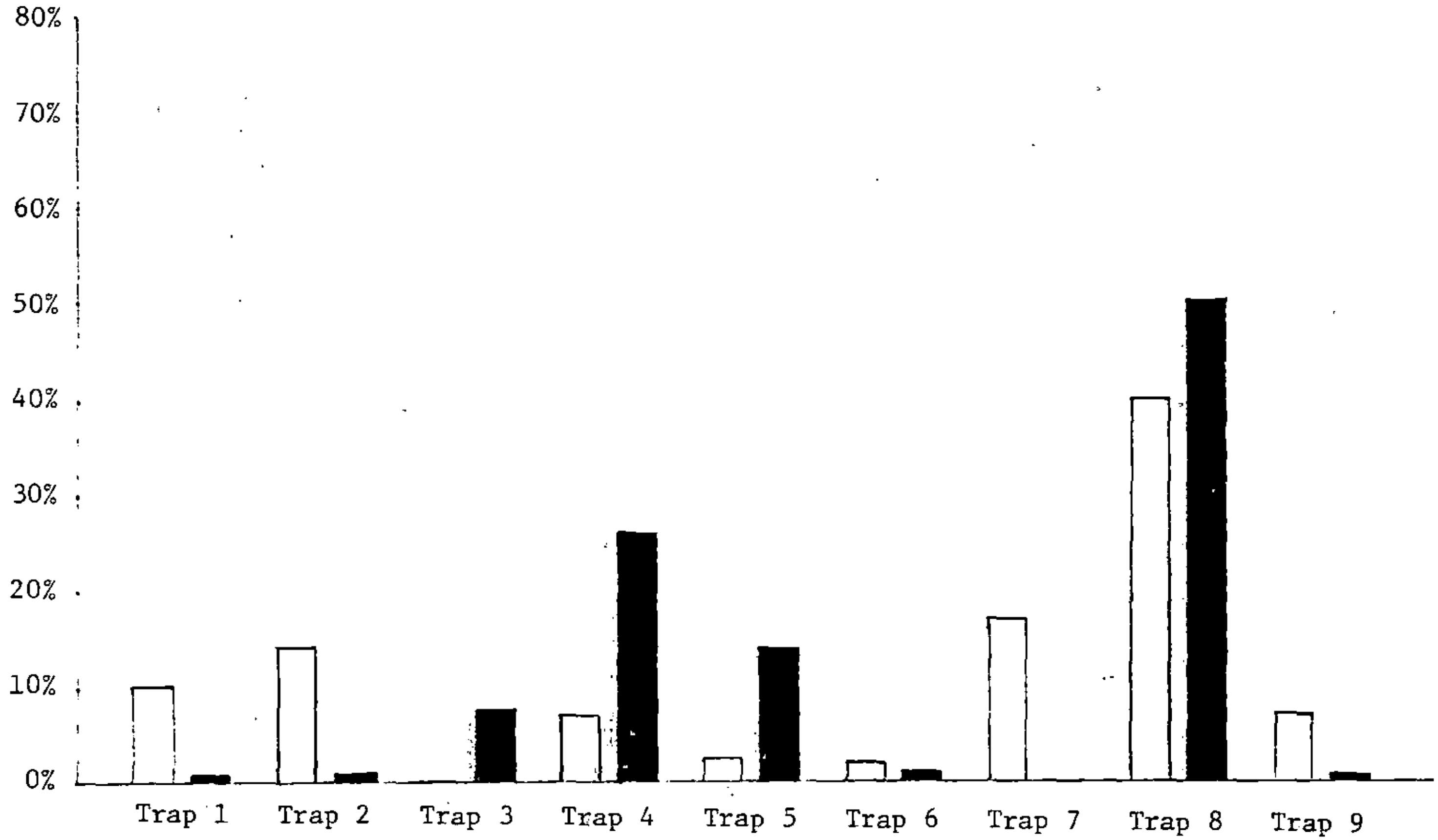


Figure 2. Population distribution of <u>Aleochara</u> sp. (unshaded bars) and <u>Atheta</u> sp. (shaded bars) in Bat Cave study station traps.

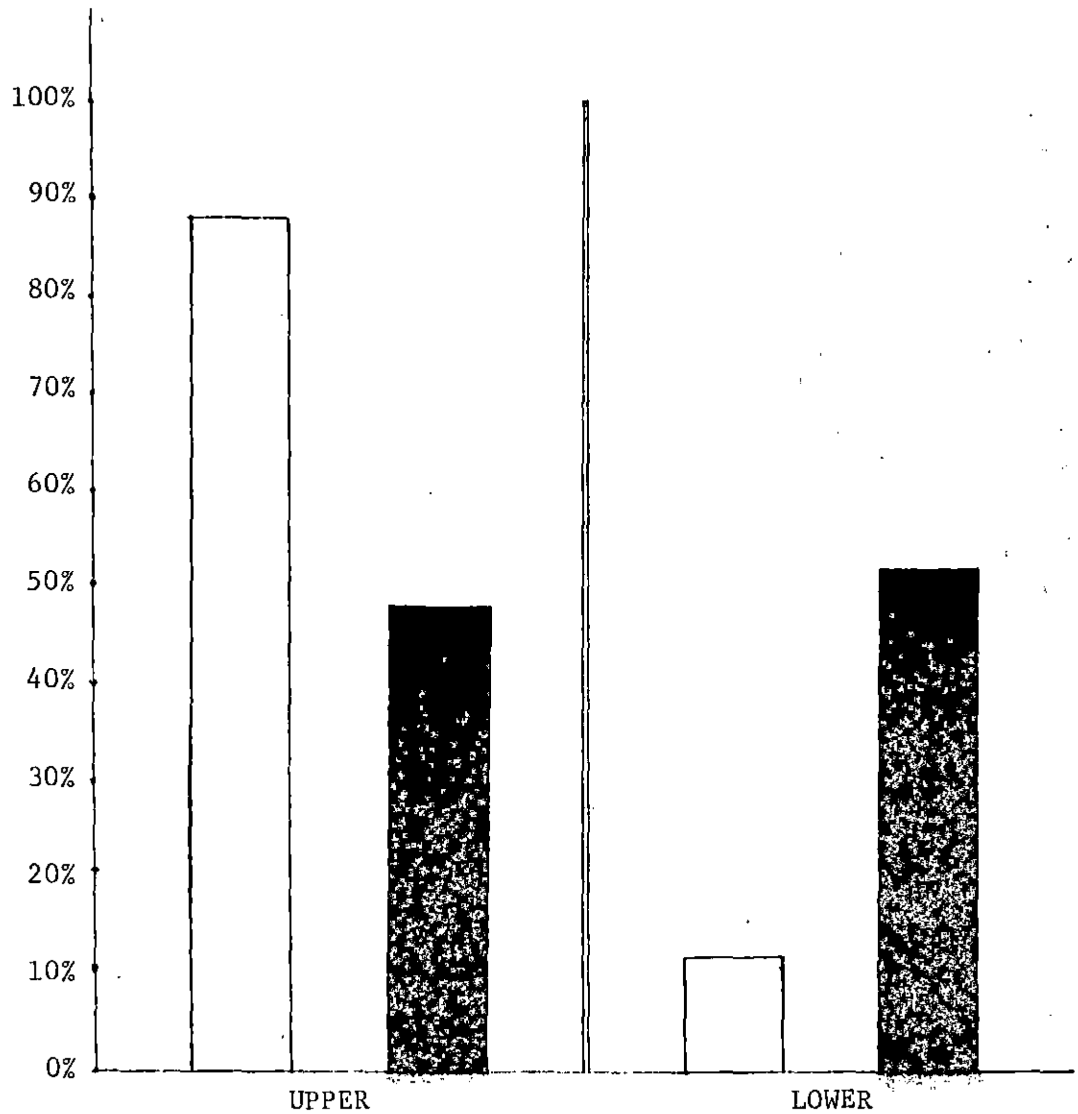


Figure 3. Population distribution of Aleochara sp. (unshaded bars) and Atheta sp. (shaded bars) between upper and lower levels of Bat Cave.

higher than the means. This probably resulted from exceptionally high food availability at Trap 8. If the data from Trap 8 collections are disregarded bacause of the presumed exceptional nature of that area, 80% of the remaining Aleochara sp. and less than 4% of the remaining Atheta sp. are shown to have occurred at other upper level stations (Figures 4 and 5). Niche separation resulting from competition for resources becomes less evident where high resource availability reduces inter-specific competition. Aleochara sp. and Atheta sp. in Bat Cave appeared to utilize spatial separation to alleviate competitive pressures, their populations becoming highly conjunct only where food availability was high. The mechanism for spatial separation of these two species was not investigated in this study, but may be an important subject for future research.

It is noteworthy that Atheta sp. was not present in large numbers in the summer bat room, despite high food content in that area. A possible explanation is that although food content is high, competition from P. opaca may effectively reduce food availability to a level where it is not actually higher than in other areas in the cave. Because Aleochara sp. occurs normally in the upper level, this would not influence

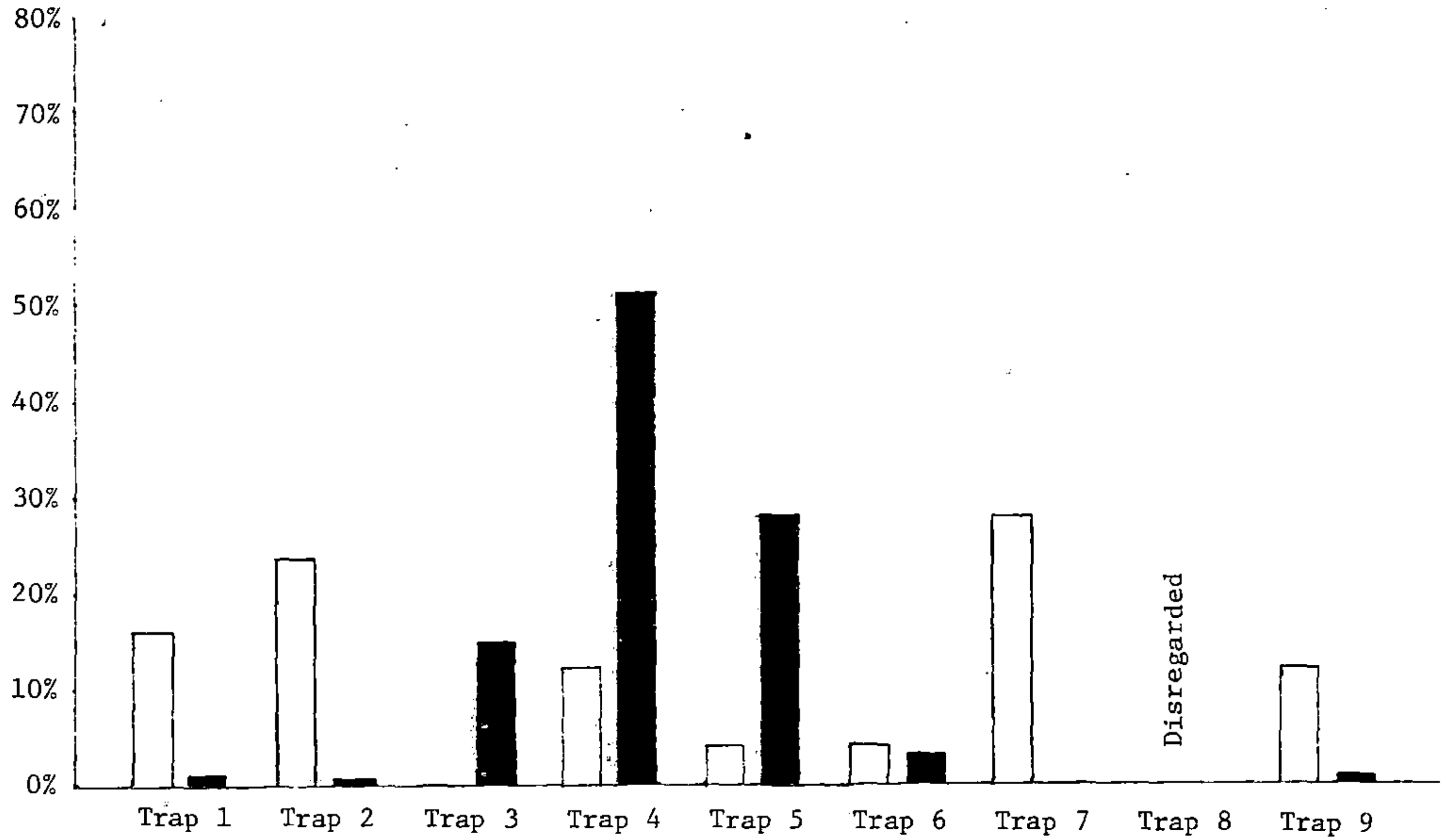


Figure 4. Population distribution of *Aleochara* sp. (unshaded bars) and *Atheta* sp. (shaded bars) in Bat Cave study station traps, disregarding Trap 8.

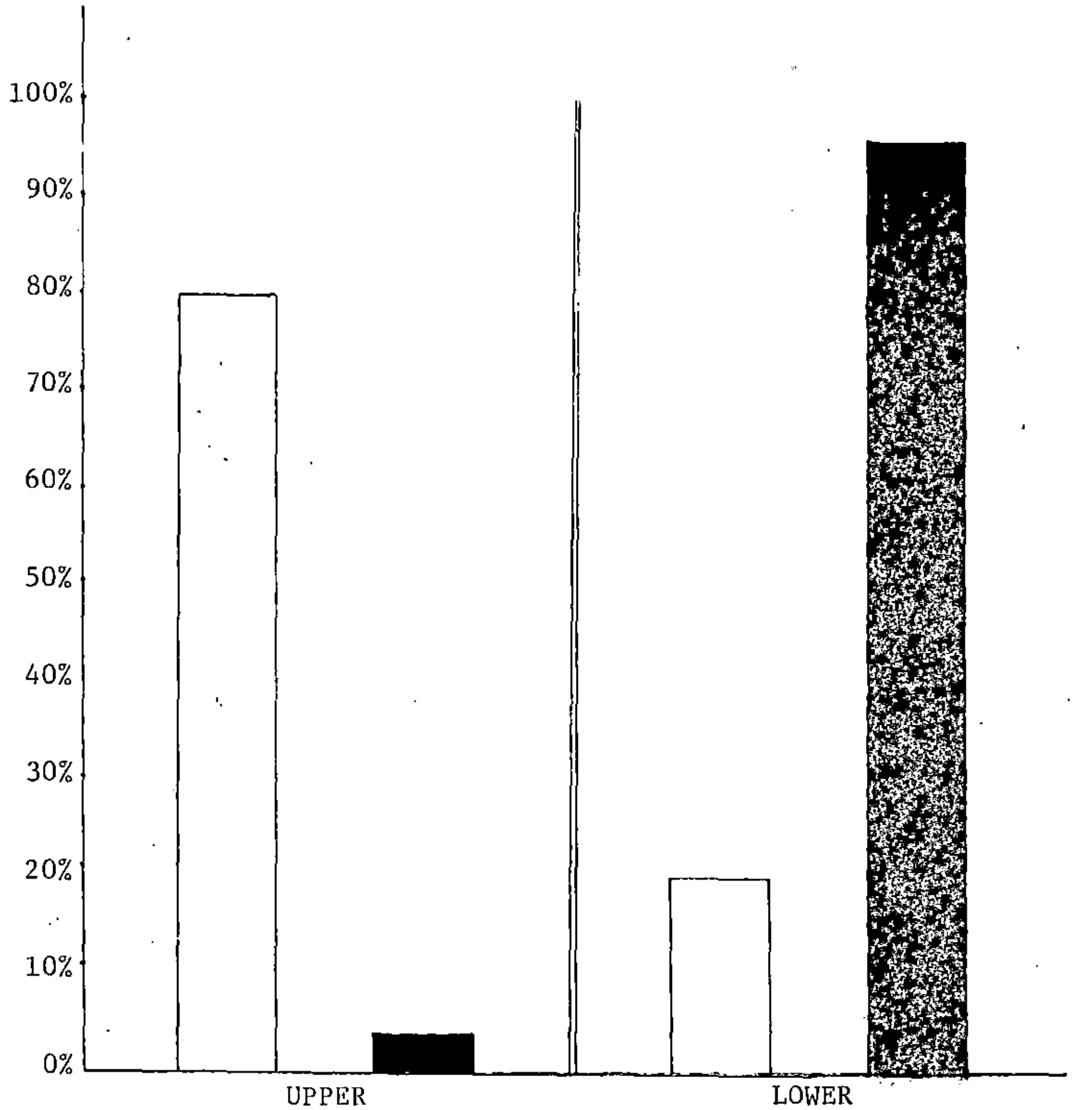


Figure 5. Population distribution of <u>Aleochara</u> sp. (unshaded bars) and <u>Atheta</u> sp. (shaded bars) between upper and lower levels of Bat Cave, disregarding Trap 8.

its distribution, whereas according to the scheme suggested here, Atheta sp. would be unable to invade the upper level in the absence of high food surplus.

The high incidence of staphylinid larvae at Trap 8 may result from high food availability, but may also be related to high temperature stability in that area (Table I).

Most ecological studies concerning cavernicolous arthropods have been concerned primarily or exclusively with troglobites. It may be that most biospeleologists are more interested in troglobites than troglophiles because of the novelty of the former. It may also be assumed that troglobites, being more highly adapted to a given habitat, are more likely to exhibit niche separation between two related species inhabiting the same area. This study was important in demonstrating a high adaptation of some troglophiles to a specific cave habitat, even to the point of distinct niche separation. Perhaps cave ecologists should give more attention to troglophilic populations in the future.

The role played by Myotis sodalis in the Bat Cave ecosystem cannot be overstated. Although stream-deposited detritus is important to some troglophiles and to the troglobite Pseudanophthalmus packardi, the most abundant beetles in Bat Cave are dependent upon the bats for food. Prionochaeta opaca and Aglenus sp. seem to be exclusively guanobic in Bat Cave, and Aleochara sp. is very nearly so. Although Atheta sp. occurred primarily in the lower level, 48% of its population was associated with bat guano near Station 8; another 25% occurred in the main M. sodalis hibernating room, where they were observed feeding on bat carcasses. Only 27% of the Atheta sp. population was actually closely associated with stream-bank detritus. This study revealed the essential role played by M. sodalis in determining the spatial and temporal distributions of cavernicolous Coleoptera in Bat Cave.

SUMMARY

Field studies were conducted from 11 July 1979 through 29 March 1980 to determine the general spatial and temporal distributional patterns of cavernicolous Coleoptera in Bat Cave.

Beetles were collected by visual survey, Berlèse extraction and pitfall trapping. Traps were set at each of nine stations located throughout the cave. Each station was described with reference to substrate type and proximity to organic materials and water supply. Temperature and relative humidity were measured at each station throughout the study period to determine their possible influence on beetle distribution. Large deposits of stream-bank detritus were observed as possible food sources for cavernicoles. The Indiana Bat, _Myotis sodalis_, which occurs in large numbers in Bat Cave, was studied to determine its role in supplying food to cavernicolous beetles via guano deposition and the contribution of carcasses.

Results show that the Bat Cave ecosystem comprises two distinct terrestrial faunal associations, each with its own characteristic beetle fauna. Those taxa reported for the first time from Carter County caves are preceded

by an asterisk (*). The lower level was characterized by a primarily xylophagous biota including the cavernicolous beetles, *Atheta sp., Bembidion wingatei, Agonum sp. #1, *Ptenidium sp., *Batrisodes sp., *Quedius spp. and Brathinus nitidus. It also included the accidentals, Agonum sp. #2, *Clivina sp., *Dyschirius sp., *Omophron americanus, Pterostichus sp., *Nemadus horni, *Dendrophilus sp., *Glischrochilus fasciatus, *Scydmaenus sp., *Homaeotarsus sp., *Psephidonus sp., *Stenus sp., *Tachinus sp. and *cantharid larvae. The rare troblobite, Pseudanophthalmus packardi, known to occur in Bat Cave, was not encountered in this study, perhaps due to its strict seasonality.

The upper level was characterized by a primarily guanobic biota including the troglophilic beetles, Prionochaeta opaca, *Aglenus sp., *Aleochara sp., *Atheta sp. and *staphylinid larvae. The upper level guanobic communities make up the bulk of the beetle fauna of Bat Cave. Results showed the presence of niche separation as a mechanism for competitive co-existence between Aleochara sp., Atheta sp. and P. opaca, indicating a high degree of cavernicolous adaptation in these troglophiles.

The role played by M. sodalis in the Bat Cave ecosystem was shown to be of vital importance to the beetle fauna; most of the beetles depend on food import by the bats.

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APPENDIX

Invertebrates other than Coleoptera collected in Bat Cave's aphotic zone during this study are listed below in phylogenetic sequence. Taxa marked by an asterisk (*) are reported for the first time from Carter County caves.

Platyhelminthes

  Turbellaria

    Tricladida

      *Sphalloplana (Speophila) sp.

        Common in upper level pools. Some in Cave Branch.

*Nematomorpha

  *Gordioidea

    *Gordiida

      *Gordius sp.

        Occasional in upper level pools.

Arthropoda

  Arachnida

    *Pseudoscorpionida

      Stream-bank detritus.

Phalangida

Sabacon cavicolens

Stream-bank detritus.

Araneae

Several unidentified species.

Ubiquitous.

Acarina

Several unidentified species.

Stream-bank detritus; guano deposits.

Crustacea

Amphipoda

**Gammarus minus*

Common in Cave Branch.

Cragonyx sp.

Common in upper level pools.

Stygobromus sp.

Common in upper level pools.

*Isopoda

**Caecidotea* sp.

Occasional in upper level pools and Cave Branch.

*Decapoda

**Cambarus* sp.

Common in Cave Branch.

*Chilopoda

Several unidentified species.

Stream-bank detritus; guano deposits.

Diplopoda

Chordeumida

Pseudotremia carterensis

Common; ubiquitous.

Order unknown

Several unidentified species.

Stream-bank detritus.

Insecta

Collembola

*Isotomidae

Stream-bank detritus; uncommon.

Sinella sp. or spp. (Entomobryidae)

Common; ubiquitous.

Tomocerus sp. (Entomobryidae)

Common; ubiquitous.

*Poduridae

Stream-bank detritus.

Onychiuridae

Stream-bank detritus.

Arrhopalites sp. (Sminthuridae)

Common; ubiquitous.

Sminthuridae (several species)

Common; ubiquitous.

Orthoptera

<u>Ceuthophilus</u> sp. or spp.

Common in lower level.

<u>Hadenoecus</u> <u>cumberlandicus</u>

Common; ubiquitous.

<u>Euhadenoecus</u> <u>putaneus</u>

Common; ubiquitous.

*Psocoptera

Stream-bank detritus.

Diptera

*<u>Chelipoda</u> sp. (Empidae)

Common in main hibernation room.

*Chironomidae

Occasional.

*Tipulidae

Occasional in lower level.

<u>Megaselia</u> sp. (Phoridae)

Common; ubiquitous.

<u>Leptocera</u> sp. (Sphaeroceridae)

Common, especially in guano deposits.

*Mycetophilidae

Occasional in lower level.

Sciara sp. (Sciaridae)

Common; ubiquitous.

Sciaridae (apterous)

Near Traps 3 and 5.

*Cecidomyiidae

One collected.

Psychoda sp.

Common at stream-bank detritus and guano deposits.

*Siphonaptera

*Leptopsyllidae

Two from Trap 8.

*Hymenoptera

*Braconidae

Three from Traps 2 and 9.